Seasonal variations in brood size of *Lasaea* cf. *nipponica* (Bivalvia: Galeommatoidea) in Hong Kong

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Abstract. Monthly samples of *Septifer virgatus* Weigmann, 1837 (Mytilidae) from an exposed rocky shore in Hong Kong were examined for *Lasaea* cf. *nipponica*. Evidence for assigning this name to the Hong Kong species of *Lasaea* is given.

Lasaea cf. *nipponica* is hermaphroditic and produces two broods of crawl-away juveniles each year, in spring (May) and autumn (October to December). Although brood size is a function of parental size, spring parents brood large numbers ($\bar{x}$ = 81.5/parent) of larger (~320-330 μm shell length) juveniles; autumn parents brood fewer ($\bar{x}$ = 24/parent) numbers of smaller (~300-320 μm shell length) juveniles. Greater variation in the size of juveniles comprising the spring broods, however, suggests that a seasonal comparison of this factor could be non-significant and requires further study.

This study suggests that variations in brood size (and possibly juvenile size) results from seasonal differences in environmental factors acting upon the parents. Brood size (and possibly juvenile size) is therefore likely to vary not just seasonally, but across the spectrum of populations encompassed by the species range.

Morton and Scott (1989) reported upon a species of *Lasaea* from Hong Kong shores and to which they ascribed the name *Lasaea rubra* (Montagu, 1803). Such a designation for a species with a presumed North Atlantic Ocean distribution (Keen, 1983) could be considered intrepid, except that Ponder (1971) believes the species to have a much wider distribution, encompassing the Pacific Ocean, than hitherto presumed, possibly because of artificial introductions. Regional workers, e.g. Habe (1977), and researchers of the Chinese marine Mollusca, e.g. Bernard *et al.* (in press), refer to the Asian species of *Lasaea* as *L. undulata* (Gould, 1861). Morton and Scott (1989) pointed out, however, that the Hong Kong species does not possess the prominent, widely spaced, concentric rings that are believed typical of *L. undulata*. Ó Foighil (1988) has, however, suggested that the presence or absence of heavy concentric rings is a poor character for separating species of *Lasaea*. The taxonomic status of the Hong Kong species of *Lasaea* will be discussed.

The Hong Kong species of *Lasaea*, i.e. *Lasaea* cf. *nipponica*, occurs amongst an ~ 1 mm wide band of mussels (*Septifer virgatus* Wiegmann, 1837) colonizing the area of mean high water neap tide (MHWNT) on exposed rocky shores. From September 1989 to August 1991, monthly samples of *S. virgatus* were inspected for *Lasaea*. These were, in turn, examined for the presence of brooded juveniles, with a view to: (a) obtaining characters which would aid in the identification of the local species of *Lasaea*; (b) reveal the pattern of reproduction and, thus, brooding undertaken by the species locally; (c) correlate features of brood and juvenile sizes with adult size to assess the extent of intraspecific variation in this species. Coincidentally, hydrological parameters were investigated so as to provide a measure of the environmental changes the local species of *Lasaea* experiences and possible correlations with such important activities as gametogenesis and the release of crawl-away juveniles.

MATERIALS AND METHODS

Each month, between September 1989 and August 1990, samples of *Lasaea* cf. *nipponica* were obtained from standard (20 x 20 cm) random samples of *Septifer virgatus* along the exposed shores at Cape d'Aguilar, Hong Kong Island. The samples were fixed immediately in 5% neutral formalin. Each individual in each sample was measured along its greatest length to the nearest 0.1 mm using a dissecting microscope and eye-piece graticule. Wherever possible, ten individuals from each 0.1 mm size class so obtained were dissected and the ctenidia inspected for brooded juveniles. When found, they were isolated from each ctenidium and counted. Each one was then measured along its greatest length to the nearest 1 μm using a compound microscope and eye-piece graticule. Numbers of juveniles in the left and right ctenidia were separated, initially, but a subsequent test for differences showed there to be none and the two sets of information were pooled subsequently to give a total figure for the numbers of juveniles/parent. The results obtained will be discussed in relation to the prevailing hydrological climate

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of Cape d'Aguilar and which was assessed by similarly monthly-obtained water samples that were analyzed in terms of temperature, salinity, pH and dissolved oxygen using standard procedures.

TAXONOMY

Bernard *et al.* (in press) record *Lasaea undulata* Gould, 1861 from the coast of China. This is considered to be the senior synonym for both *L. nipponica* Keen, 1938 and *Kellia minutissima* Habe, 1960 (Habe, 1977). Morton and Scott (1989), however, reported upon *L. rubra* (Montagu, 1803) from Hong Kong, noting the lack of strong concentric rings in local specimens but which are, apparently, characteristic of *L. undulata* (Keen, 1938). As this study will later show, however, the Hong Kong *Lasaea* is quite unlike *L. rubra* in terms of breeding season and brood size. Ó Foighil (1989) has suggested that the Hong Kong species of *Lasaea* produces crawl-away juveniles; this study will confirm that observation. Ó Foighil (1989) further points out that the species of *Lasaea* found in Kagoshima, Japan, referred to as *L. undulata*, produces planktotrophic larvae and appears to be identical, in terms of valve morphology, to the similarly planktotrophic Australian species *L. australis* (Lamarck, 1818). Ó Foighil (1989) further points out that in Kagoshima, there appears to be two species of *Lasaea*, one with planktotrophic larvae (*L. undulata*?) and one with crawl-away juveniles. In Japan, Taiwan and Hong Kong, species of *Lasaea* also have crawl-away juveniles. Keen (1938) compared her species, *L. nipponica*, from Japan with two other species, also from Japan, i.e. *L. striata* Tokanuga, 1906 and *L. undulata*, and dismissed both as possible conspecifics, the former being far too big (9.5 mm shell length), the latter too heavily ringed concentrically. *L. undulata* with a maximum shell length of ~ 5 mm is also larger than *L. nipponica* (2.9 mm shell length). The largest individual of the Hong Kong species of *Lasaea* ever found is 4.0 mm long, reproductively mature parents falling between 2.1 - 3.6 mm in shell length. Thus, in terms of shell form and size and the degree of concentric ringing, the Hong Kong species is most like *L. nipponica*. If it is true, moreover, that *L. undulata* produces planktotrophic larvae, whereas the second widely distributed species in Japan (plus Taiwan) produces crawl-away juveniles, then it seems possible that this species, and the Hong Hong species, is *L. nipponica* and is distinct from *L. undulata* despite its synonomy with the former species by recent workers, e.g. Habe (1977). In the absence of good comparative data it has, however, been confused with *L. undulata*, the latter name eventually coming to gain widest coinage. For the above reasons, I refer here to the Hong Kong species as *Lasaea* cf. *nipponica*. Scanning electron micrographs of two paratypes of *L. nipponica* are illustrated in figures 1A and B (California Academy of Sciences Reg. No. 7227 and 7228, respectively) (Invertebrate Zoology Cat. No. 065920). These individuals were collected from Watanoha, Rikuzen, N.E. Matsusima, Honshu, Japan by S. Nomura. A scanning electron micrograph of an individual of *Lasaea* cf. *nipponica* from Cape d'Aguilar, Hong Kong is illustrated in figure 1C. They appear to be conspecific. Subsequent information on the reproductive biology of *L.* cf. *nipponica* in Hong Kong will, hopefully, provide for a better interpretation of this species and allow separation of it from others.

RESULTS

Figure 2 shows the numbers of individuals of *Lasaea* cf. *nipponica* obtained from the standard *Septifer virgatus* samples over the course of one year from September 1989 - August 1990. Two peaks are obvious, the first in January 1990, the second in May 1991, when densities were ~ 1750 m^2

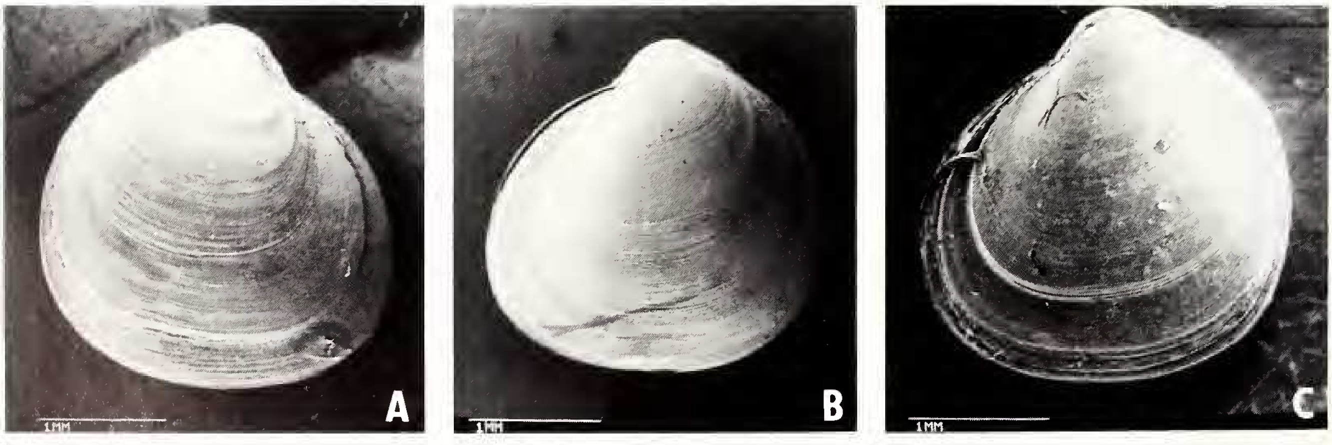

Fig. 1. A, B. Two paratypes of *Lasaea nipponica* (Keen, 1938) from Honshu, Japan (CAS Reg. No's. 7227 and 7228, respectively). **C,** *Lasaea* cf. *nipponica* from Cape d'Aguilar, Hong Kong.

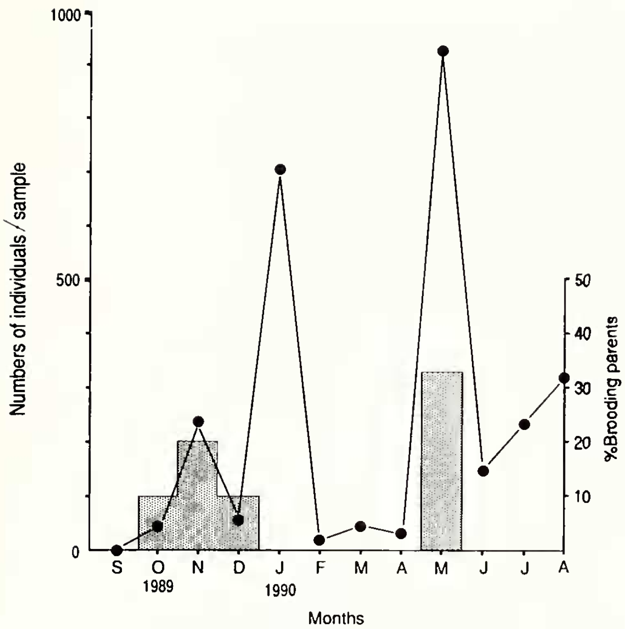

Fig. 2. *Lasaea* cf. *nipponica*. Numbers of individuals obtained in each monthly sample from *Septifer virgatus* beds at Cape d'Aguilar, Hong Kong (stippled areas indicate the % number of brooding parents in each sample).

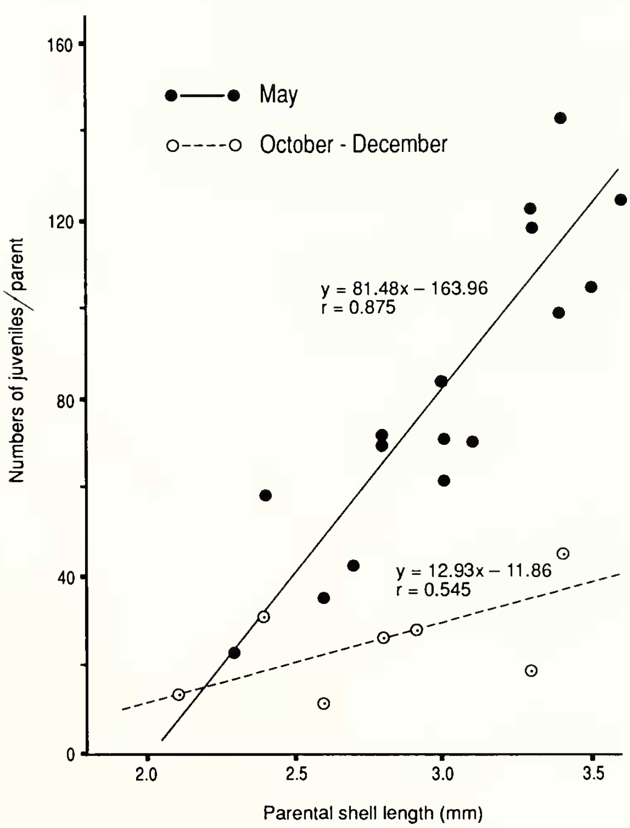

Fig. 3. *Lasaea* cf. *nipponica*. The numbers of juveniles/parent, expressed as a function of parental shell length, for both spring (May) and autumn (October - December) broods in Hong Kong.

and 2375 m^{-2}, respectively. At other times of the year, densities were low, all < 600 m^{-2} and for most of the time < 125 m^{-2}. Overlain on figure 1 is the incidence of brooding individuals. Peaks in overall numbers in the population thus match peaks in the incidence of brooding. Juveniles were obtained from *L.* cf. *nipponica* parents in October, November and December 1989 and in May 1990, with the latter month providing the greatest % of brooding individuals, i.e. > 36%.

Figure 3 compares the data obtained for parental shell length and numbers of juveniles/parent. As might be expected, brood size in both seasons is a function of parental size; bigger parents have bigger broods. From October to December, brooding individuals of up to 3.4 mm shell length were obtained with a mean of 24 shelled juveniles/parent and a maximum of 44 juveniles/parent, of 4.4 mm shell length. In May 1990, the picture was different, brooding individuals of up to 3.6 mm shell length were obtained with a mean of 81.5 juveniles/parent, although a maximum number of 151/parent, of 3.3 mm shell length, was recorded. Obtained values for brood sizes between the two periods have been tested for significance using an Analysis of Variance and are significantly different (F = 19.835; P < 0.001).

Figure 4 compares the data obtained for parental shell length (mm) and juvenile length (μm). In May 1990, average juvenile shell length, for each 0.1 mm increase in parental shell length, ranged between 308-335 μm. From October to December, values ranged between 298 and 323 μm. Juvenile shell length, at both times of the year, did not increase with

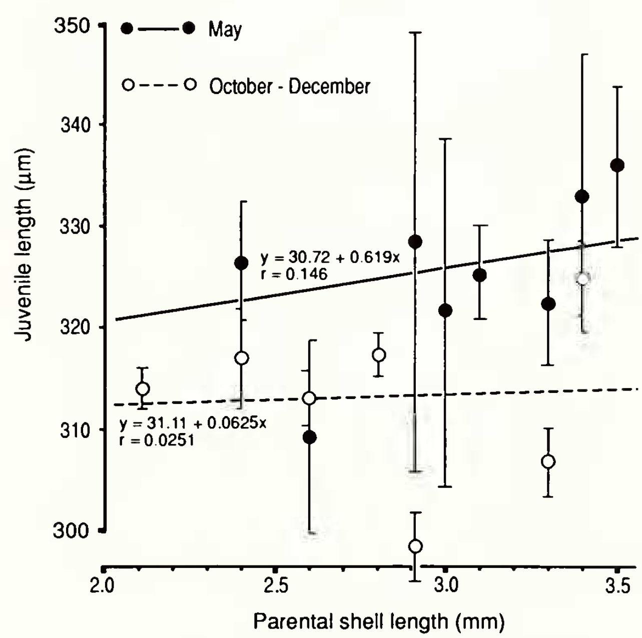

Fig. 4. *Lasaea* cf. *nipponica*. Juvenile shell length, expressed as a function of parental shell length, for both spring (May) and autumn (October - December) broods in Hong Kong (mean ± 1 S.D.).

parental shell length, i.e. bigger parents did not have bigger juveniles. Such data are significantly different ($P = 0.05$).

Figure 5 compares juvenile length (μm) and numbers of juveniles/parent. For May 1990, a mean juvenile length of 325 μm was obtained which did not vary significantly with respect to the numbers of juveniles present. From October to December, mean juvenile lengths varied between ~ 300-310 μm, with an apparent decline in length with increasing numbers. This decline is not, however, statistically significant although it is true that the two sets of seasonal data are significantly different ($P = 0.05$).

The results obtained from this study suggest that spring parents (May) brood larger numbers ($\bar{x} = 81.5$/parent) of bigger juveniles (~ 320-330 μm); autumn parents (October - December) brood fewer ($\bar{x} = 24$/parent), smaller (~ 300-320 μm), juveniles. The large standard deviations in juvenile shell lengths (Figs. 3 and 4), however, cast doubt on the significant difference obtained for the data between the two seasons. Note, for example in figure 4, the wide standard deviations in juvenile shell lengths obtained for spring parents of 2.6, 2.9, 3.0 and 3.4 mm shell length. This would suggest that in May, a variety of developmental stages were present in the broods whereas from October - December, broods were more uniformly at a similar stage of development.

DISCUSSION

Species of the cryptic galeommatoidean genus *Lasaea*, occupy the high intertidal virtually world-wide and have aroused interest because of their smallness (< ~ 5 mm), their adaptations to such a high-zoned life (Ballantine and Morton, 1956; Morton, 1956, 1960; Morton *et al.*, 1957) and their mode of reproduction, i.e. simultaneous hermaphroditism and self-fertilization, with ctenidial brooding (Oldfield, 1955; Ó Foighil, 1987; Ó Foighil and Eernisse, 1988). Seed and O'Connor (1980) followed seasonal changes in population structure of *Lasaea rubra* on the north-east coast of Ireland and suggested that the population comprised three to four age groups, but with few individuals living beyond their third year. McGrath and Ó Foighil (1986) also studied the population dynamics of *L. rubra* in south-east Ireland and showed essentially the same pattern, i.e. the polymodal population picture suggested a life span of 2-3 years, with only a few individuals entering their fourth year.

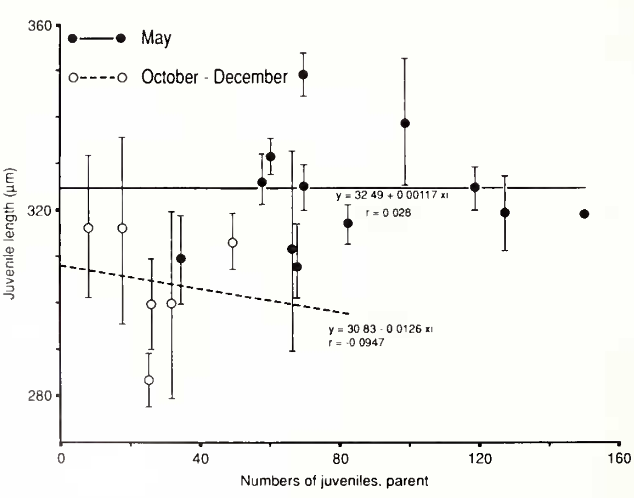

Fig. 5. *Lasaea* cf. *nipponica*. Juvenile shell length, expressed as a function of the numbers of juveniles/parent, for both spring (May) and autumn (October - December) broods in Hong Kong (mean ± 1 S.D.).

The work of Oldfield (1964), Seed and O'Connor (1980) and McGrath and Ó Foighil (1986) all suggest that *Lasaea rubra* in the British Isles reproduces in a single phase over summer, typically from May to October, with maximum numbers of brooded, crawl-away, juveniles occurring from June-July and with peak recruitment occurring in August. Oldfield (1964) studied the life cycle of *L. rubra* in south-west England and estimated an incubation period of about two months. McGrath and Ó Foighil (1986) have summarized the literature on reproduction in *L. rubra* and of other species, notably *L. subviridis* from the north-east Pacific. The latter species broods juveniles year round but with peaks occurring at different times of the year, according to location. *L. rubra hinemoa* (from New Zealand) and *L. australis* (from Australia) similarly brood juveniles year round (Booth, 1979; Roberts, 1984).

Table 1 summarizes the data on the above species of *Lasaea* and compares it with information obtained about the species reported upon in this study. The Hong Kong species of *Lasaea* shows some similarities with other species, e.g. the maximum size of brooding adults (3.6 mm) approximates that recorded for *L. subviridis* (Glynn, 1965; Ó Foighil, 1985; Beauchamp, 1986). In other respects, however, notably with regard to the juveniles, the species is distinct, i.e. brood size ranges from means of 24 - 81.5/parent, in autumn and spring, respectively, whereas for other species it is far fewer. Similarly, crawl-away juvenile length is approximately half that of the other species hitherto investigated. Moreover, the local species broods juveniles in two phases, i.e. spring and autumn, whereas *L. subviridis* broods juveniles year round (Ó Foighil, 1985) and *L. rubra*, in the north-eastern Atlantic, is a summer brooder (Oldfield, 1955, 1964; Seed and O'Connor, 1980; McGrath and Ó Foighil, 1986). *L. rubra* does, however, brood over the same time frame as *L.* cf. *nipponica* in Hong Kong, i.e. from May - ~ November.

Russell and Huelsenbeck (1989) report upon variations in brood size and brood structure in the small venerid bivalve *Transenella confusa* Gray, 1982, from California. In this species, although broods are present in some individuals throughout the year, brood size was significantly lower in winter although it is also a function of adult length (as shown here for *Lasaea* cf. *nipponica*). Moreover, the relative pro-

Table 1. Aspects of the reproductive biology of species of *Lasaea* (after McGrath and Ó Foighil, 1986) compared with those identified for *L.* cf. *nipponica* from Hong Kong.

Species	*Lasaea rubra*	*L. subviridis*	*L. rubra hinemoa*	*L.* cf. *nipponica*
Expression of sexuality	hermaphroditic	hermaphroditic	hermaphroditic	hermaphroditic
Brooding period	summer	year round	year round	two phases (May, October - December)
Brood size (juveniles/parent)	6-22 1-21	2-39 4-30	2-33 4-71	$\bar{x}$ = 24 (autumn) $\bar{x}$ = 81.5 (spring)
Maximum size of brooding adult (mm)	2.4	3.3-3.5	4.1	3.6
Size of released juveniles (μm)	500-600	530-650 600-700	500-600 510-640	280-340
	Oldfield, 1955; Seed and O'Connor, 1980	Glynn, 1965; McGrath and Ó Foighil, 1986	Booth, 1979; Beauchamp, 1986; Ó Foighil, 1985	this study

portions of developmental stages within the broods of *T. confusa*, varied seasonally, as is possibly the case with *Lasaea* cf. *nipponica* in Hong Kong, suggesting variation due to environmental factors.

In Hong Kong, many subtropical species of bivalves show two phases of recruitment, in spring and autumn, e.g. the freshwater species *Limnoperna fortunei*, *Corbicula fluminea* and *Musculium lacustre* (Morton, 1987) as well as the estuarine species, *Brachidontes variabilis*, *Saccostrea cucullata* and *Gafrarium pectinatum* (Morton, 1988, 1990a,b). A similar pattern is emerging for marine intertidal species, e.g. *Septifer virgatus* (Morton, unpub. data). It is thought possible that an otherwise single peak of reproduction is divided into two, early and late, phases by either high mid-summer temperatures or low salinities as a result of the impact upon Hong Kong of the tropical south-east Monsoon (Morton, 1991). In the case of the freshwater species, summer rain-induced flooding can flush away gametes or newly-released juveniles. Such a suggestion needs verification and is being investigated. If it is true, however, then the local species of *Lasaea*, i.e. *Lasaea* cf. *nipponica*, could be compared with *L. rubra* in terms of a summer peak in reproduction being divided into early and late phases by environmental extremes. Sea water temperatures in Hong Kong in May and from October - December are, however, far higher than these reported to be optimal for reproduction in both *L. rubra* (~ 7°C - 14.5°C) (Seed and O'Connor, 1980; McGrath and Ó Foighil, 1986), to which it has been compared (Morton and Scott, 1989), and *L. subviridis* (8 - 15°C) (Ó Foighil, 1985) and range between 26°C (May) and 28°C declining to 19°C between October and December. Salinity, pH and dissolved oxygen levels are less variable during the brooding months than at other times of the year (Table 2).

Similarly, with regard to the numbers of brooded juveniles ($\bar{x}$ = 24 - 81.5/parent) and their maximum size (280-340 μm), the local species is different from all other species of *Lasaea* for which information is available (Table 1). In comparison with all other species, *Lasaea* cf. *nipponica* in Hong Kong broods, approximately, twice the number of half the size juveniles.

On the basis of earlier described taxonomic evidence and the data set out above, it is, therefore, concluded that the local species of *Lasaea* is best designated the name, *Lasaea* cf. *nipponica*.

Ó Foighil (1986) has shown that *Lasaea subviridis* can brood juveniles to either the Prodissoconch I or Prodissoconch II stage (Carriker and Palmer, 1979; Waller, 1981), the former lacking and the latter possessing commarginal striae. Ó Foighil suggests that prodissoconch morphology is environmentally regulated such that the former morphology is produced by submerged adults, the latter by intertidal parents. This study similarly suggests that for *Lasaea* cf. *nipponica*, juvenile size is different for spring and autumn

Table 2. The ranges of various sea water parameters at Cape d'Aguilar, Hong Kong, and those prevailing during the periods (May and October - December) when *Lasaea* cf. *nipponica* is brooding juveniles.

	Range	May	October - December
Temperature (°C)	17-30	26	28-> 19
Salinity (‰)	26-33	32	31-32
pH	7.7-8.4	8.1	8.3-8.1
Dissolved oxygen (mg/l)	5.6-7.8	6.8	6.0-6.9
Most probable wave heights (m) (50% exceedance) (After Apps and Chen, 1973)		2.0	2.9

clutches. This observation, however, due to the great variation in the sizes of juveniles comprising, particularly, the spring broods, requires further verification and such data need to be thus treated with caution. In Hong Kong, however, wave heights are higher in autumn than in spring (Apps and Chen, 1973) (Table 2) although the pattern of tidal fluctuations is similar at these times of the year (Morton and Morton, 1983). Autumn parents are thus more frequently immersed (by higher waves) than spring parents. It is thus possible that brood size (and possibly juvenile size) is related to immersion period which, if true, is similar to the situation reported upon by Ó Foighil (1986) for *L. subviridis*. Russell and Huelsenbeck (1989) similarly show for *Transenella confusa* in California that brood size is smaller in winter than at other times of the year.

Brooded juveniles of *Lasaea* do not possess feeding structures (Oldfield, 1964; Beauchamp, 1986; Ó Foighil, 1986). It is, therefore, likely, since the parental size range is the same in spring and winter, that differential environmental factors act upon the *Lasaea* cf. *nipponica* parents in spring and summer to limit brood size in winter. This could be because of seasonal differences in percentage time immersed, acting via seasonal variations in wave height (Table 1). It is possible that such factors act upon the physiological environment of the parental mantle cavity, as suggested for *Ostrea edulis* by Waller (1981) and *L. subviridis* by Ó Foighil (1986).

The results of this study upon *Lasaea* cf. *nipponica* and that of Russell and Huelsenbeck (1989) upon the burrowing *Transenella confusa* suggest that brood size is environmentally regulated. So, apparently, is prodissoconch morphology in *L. subviridis*. Apart from the obvious implications of the former observations with regard to subsequent recruitment and thus population dynamics, such studies collectively suggest that the wide variation in shell form typical of species of *Lasaea* is phenotypic, accounting for the many taxonomic problems surrounding the representatives of this genus.

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